

Pattern of Genetic Diversity of Feral domestic cat populations in Lamu, Kenya and Iran suggest possible influence of historical trade between Persian Gulf and East African Coast

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Abstract

Background: During Early Indian Ocean trade, many species of animals were transported along the routes and destinations especially in eastern Africa. The influence of this historical trade on genetic relationships of historically popular pets such as domestic cats, in East African Coast and Persian Gulf has never been evaluated. Herein, we analyzed variation in mitochondrial DNA sequences from one African wildcat together with 59 feral and domestic cats from East African coastal-Lamu (EAC-Lamu) (n=41) and Iran (n=18) to evaluate possibility of exchange of these animals during the historical trade.

Results: From this analysis, all *ND5* & *ND6* sequences of EAC-Lamu and Iranian cats can be assigned into one haplogroup. The haplotype sharing pattern between these two regions is detected in the network. The whole genome analyses reveal cats from EAC-Lamu and Iran cluster into one branch whereas other cat breeds cluster separately into other branches. The demographic history inference further confirms the relationship between EAC-Lamu and Iranian indigenous cats split around 2,800 years ago, followed by gene flow as a result of human activities.

Conclusions: Our results unveil the diversity and existing relationship between indigenous cats from Iran and EAC-Lamu due to historical trade. The current data do not permit us to make further conclusions; therefore, more research evidence from genetics and archaeology may provide further insights into the direction of genetic influence of this historical trade.

1. Background

The world's domestic cat, *Felis catus*, is tamed form of wild cats, *Felis sylvestris* [1] Combinations of archeological and genetic evidence suggest that origin of domestication of *Felis catus* occurred independently from three subspecies of *Felis sylvestris*. These three progenitors comprise *Felis sylvestris libyca* in Africa, *Felis sylvestris sylvestris* in Europe and *Felis sylvestris ornata* from Near East Asia [1–3], during Neolithic revolution around 10,00–9,500 years ago [2, 4]. Since then domestic cat has spread to all corners of the World. Today it is the World most popular and common household pet despite playing the least role in the direct survival of human [2, 5]. The history of domestic cat has already been highlighted in a number of studies showing evidence in patterns of genetic variations [2].

There are three interacting factors that have shaped the genetic evolution of domestic cat breeds in all its range Worldwide. The first factor is the transition from wild cat through commensal or symbiotic life around human settlement to a fully household pet artificially bred by human. As a pet the cat's breeding is artificially selected by human primarily for aesthetically appealing phenotypic traits [6]. The second factor is the reproductive interaction between the household pet with wild relatives and feral ones living around homesteads but not in houses. This is a situation in which some household cats escape to streets, farms, bushes around homesteads (feral) and become unattached to any household or owner. They interbreed among themselves, also with household populations and back with wild relatives as has been shown in Europe [2]. The third factor that has influenced genetic pattern of domestic cat breeds is

scale of gene flow perpetrated by human during long distance movement. The genetic significance of this must have been greatest at the early stages of domestication when hypothetically Asian subspecies (*F. s. ornata*) was transported to and interbred with African one, *F. s. libyca* or European one, *F. s. sylvestris*[2, 7]. Over 50 domestic cat breeds known in the world today are products of these interacting factors.

Despite this good breadth of knowledge especially on genome[7–10], biology and breeds[1, 6, 8, 11–15], significant paucity still remains in our knowledge regarding influence of long distance trade on genetic diversity of domestic cats in Near East Asia and east African coast where currently feral populations are common.

Archeological evidence suggests that Levant region (Near East) is the epicenter of cats domestication around 9,500 years ago before spreading to other parts of Asia, and possibly through trade in Europe and Africa[2]. Similarly, archeological studies especially on iron tools [16] and other cultural artifacts [17] have demonstrated interaction between Persian and East African coastal (EAC) people in the 11th century [18]. It is possible that domestic cats were transported to EAC, especially Lamu which has been described by historian and archeologists as the epicenter of old trade. In this trade, networks there were on one side, pastoralists, hunter gatherers and farmers from African hinterland, and Persian Gulf and India communities on the other hand. In this interaction, domestic cats are likely to have been moved as pets from Persian Gulf, Oman and India by traders to Lamu, where cats currently exist largely as feral populations around villages. It is also possible that hinterland feral or household cats were moved to Lamu and EAC in general and finally to Persia. The current domestic cat community in Lamu therefore could be a constellation of genes from African hinterland and Levant regions.

In this study, we examined genetic diversity among and between domestic cats living as feral in East African coastal-Lamu (EAC-Lamu) and Persian Gulf-Iran to illuminate into influence of historical trade between these regions on the genetic diversity of these common and popular pet.

2. Materials And Methods

2.1. Sampling and DNA extraction

Peripheral blood samples were collected by local veterinarian from 59 wildcat and domestic cats with the consent of the local village administrations (Additional file 8: Table S1). Among these samples, 40 individuals were collected from villages in off-shore islands making Lamu complex in the EAC, Kenya after obtaining authorization for research from the Department of Veterinary Service of Kenya (RES/POL/VOL.XX.VII/162); 18 Iranian feral cats (including eight samples from the north and 10 samples from the south of the country) were collected. All experimental procedures were approved by the Animal Care and Use Committee of Kunming Institute of Zoology (SMKX2017007). The methods were carried out in accordance with the approved guideline. Additional single tissue was extracted from Wild cat captured by B. A. during small carnivore survey in Central Kenya. This particular animal was collected as voucher specimen and deposited in National Museums of Kenya.

2.2. Analysis of mitochondrial genome sequences

Genomic DNA was extracted from whole blood of 59 wildcat and domestic cats by the standard phenol/chloroform method. Protocols for PCR amplification and sequencing of *ND5* & *ND6* and D-loop region of the mitochondrial DNA (mtDNA) genome are provided in appendix (see Appendix-supplementary material and methods for details). Both light and heavy chains were sequenced. Electropherograms for the sequences were visualized, edited and aligned by SEQMAN PRO of LASERGENE 7.1.0 (DNASar, USA) against the reference sequence NC_001700[13]. The variants in the *ND5* & *ND6* and D-loop sequences were scored relative to the reference sequence NC_001700 [13].

2.2.1. *ND5* & *ND6*

The *ND5* and *ND6* comparative diversity study involved 143 DNA sequences [2] downloaded from GenBank [GenBank: information is available Additional file 9: Table S2]. All 199 sequences (56 *de novo* [GenBank: MN313723 – MN313781] and 143 from GenBank range 2300 - 2527 bp) were aligned and trimmed to 2363 bp for analysis. The 199 *ND5* & *ND6* sequences were initially aligned with CLUSTALX 2.1[19] and then checked by eye. Comparisons of sequences and identification of haplotypes were performed using D_{NA}SP 5.10.1[20]. The model of substitution and related parameters were determined through Bayesian information criterion [21] in JMODELTEST 2.1.4[22]. Maximum likelihood (ML) tree was constructed from the 199 sequences data (Additional file 9: Table S2) to visualize overall similarity using MEGA6 [23] with TN93+I+G model of substitution selected by AIC in JMODELTEST 2.1.4. To discern possible genetic relationship between EAC-Lamu and Iranian cats with other Near East and Central Asia cats, ML tree was constructed based on 159 sequences (56 *de novo* and 103 from Group IV). A median-joining network[24] for the 122 haplotypes from 159 sequence data (56 *de novo* and 103 from GenBank) of wild and domestic cat samples from EAC-Lamu, Iran and group IV was constructed with NETWORK 4.6.11 (<http://www.fluxus-engineering.com>).

2.2.2. D-loop

Similarly, for comparative D-loop mtDNA diversity study for the evidence of gene flow, 75 previously sequenced cats DNA sequences[25, 26] were retrieved from GenBank [GenBank: AJ441317-AJ441319, AJ456977, AF348642, AB480177-AB480198, AB121148-AB121194] (Additional file 9: Table S2). All 129 sequences (54 *de novo* [GenBank: MH513143 – MH513196] and 75 from GenBank range 415-546bp) were aligned and trimmed to 417 bp for analysis.

The 129 D-loop sequences were initially aligned with CLUSTALX 2.1 [19] and then checked by eye. Comparisons of sequences and identification of haplotypes were performed using D_{NA}SP 5.10.1[20]. The model of substitution and related parameters were determined through Bayesian information criterion [21] in JMODELTEST 2.1.4 [22]. ML tree was constructed from the 129 D-loop data (Additional file 9: Table S2) to visualize overall similarity using MEGA6 [23] with TrN+G model of substitution which was the best model estimated by JMODELTEST 2.1.4. A median-joining network [24] for the 82 wild and domestic cat haplotypes was constructed with NETWORK 4.6.11 (<http://www.fluxus-engineering.com>).

2.3. Analysis of whole genomes

According to the *ND5* & *ND6* network, eight samples (representing four EAC-Lamu and three Iranian samples sharing similar haplotypes; including the wild cat from Central Kenya) were selected for whole genome resequencing. The sequencing data from this study have been submitted to the Genome Sequence Archive (GSA, <http://gsa.big.ac.cn/>) under project number XXXXXXXX. Details on whole genome sequencing, sequence data preprocessing and variant calling are in Appendix-supplementary material and methods. We also incorporated 11 published whole-genome sequencing data of domestic cat (consisting of three Persian cat, two American cats, two Abyssinian cats, three DovenRex cats and one Bengal cat) (<http://felinegenetics.missouri.edu/99lives>)[27](Additional file 10: Table S3). These samples cover ranges of domestic cat breeds from different regions. Maximum-likelihood phylogenetic tree was built using the 19 cat genome by FastTree 2[28] (Additional file 10: Table S3).

2.4. Estimation of Demographic History

We used the Pairwise Sequentially Markovian Coalescence (PSMC) methods developed by Li and Durbin [29] to infer trajectory of the ancestral population of both wild and domestic cat genomes in response to Quaternary climatic change. PSMC has high false-negative rates at low depth, resulting in a systematic underestimation of true event times. Therefore, we selected resequencing data of cat genomes with the highest read depth (Additional file 10: Table S3). We further performed G-PhoCS [30] to infer the population history of wild cat, EAC-Lamu and Iranian cats cat as follows. First, we split the whole-genome into segments with 1kb length. Next, we removed the regions with gaps less than 50 bases. Segments located in repeats regions were removed. Finally, we filtered the regions 50kb close with genes. Due to the long running time, we randomly selected 5,000 segments from all neutral regions. 10,000,000 iterations were then performed.

3. Results

A total of 199 *ND5* & *ND6* (56 *de novo* and 143 from GenBank) and 129 D-loop (including 54 *de novo* and 75 downloaded from the GenBank) sequences of wild cat and domestic cat samples were analyzed respectively.

3.1. MtDNA genetic diversity analysis

3.1.1. *ND5* & *ND6*

The 159 *ND5* & *ND6* Group IV sequences were assigned into 122 different haplotypes (Additional file 11: Table S4) with distribution of the two most frequent haplotypes (H_9 and H_10) in domestic cat samples from EAC-Lamu, Iran, Near East and Central Asia (Group IV). Haplotype H_13 is unique only in domestic cat from EAC-Lamu and Iran (Additional file 12: Table S5). Similarly, 129 D-loop sequences were classified into 82 distinct haplotypes (Additional file 13: Table S6). The two most frequent haplotypes, H_2 and H_3 occurred in cat samples from EAC-Lamu, Iran and Europe (Additional file 12: Table S5 &

Additional file 13: Table S6). There are 14 and seven haplotypes unique to EAC-Lamu and Iran respectively.

3.2. *MtDNA phylogenetic analysis*

ML tree (Additional file 1: Figure S1 & Additional file 2: Figure S2) obtained from 199 *ND5* & *ND6* sequences (56 *de novo* and 143 from GenBank) revealed the previously defined groups I-VI[2] and the clustering of wild cat and domestic cat samples from EAC-Lamu and Iran within the Near East and Central Asia group (Group IV). The ML (Additional file 3: Figure S3 & Additional file 4: Figure S4) for wild cat and domestic cat samples from EAC-Lamu, Iran with Near East and Central Asia further supports this relationship. ML tree (Additional file 5: Figure S5 & Additional file 6: Figure S6) was obtained from 129 D-loop data. All the domestic cats from EAC-Lamu and Iran were distributed within other domestic cats. The wild cat from EAC-Central Kenya (about 600km west of Lamu) clustered with Spanish wild cat.

3.3. *MtDNA network analysis*

Network of 122 haplotypes identified among the 159 *ND5* & *ND6* sequences further confirmed the relationship of cat from EAC-Lamu, Iran and Near East and Central Asian populations (Figure 1). Two haplotypes (H_9 and H_10) were shared among these three populations and one haplotype (H_13) between domestic cats from EAC-Lamu and Iran (Additional file 11: Table S4). The wild haplotype (H_14) was only observed in an individual from EAC-central Kenya. The network constructed from 82 D-loop haplotypes further displayed the relationships of wild cat and domestic cats between EAC-Lamu and Iran as well as with Spanish cats (Additional file 7: Figure S7).

3.4. *Phylogenetic analyses of whole genome data*

We performed whole-genome sequencing to an average depth of 28× for each of the eight samples after removing PCR redundancy (Additional file 10: Table S3). A total of 19 whole-genome sequencing data of cat (consisting of eight *de novo* and 11 downloaded from the GenBank (Additional file 10: Table S3) were analyzed. After strict filtering, we identified ~28.2 million autosomal SNPs for further analysis (Supplementary material and method).

The maximum-likelihood phylogenetic analysis revealed that at the base of the tree Iranian and EAC-Lamu indigenous cats together with other domestic cat breeds were separated from the EAC-Central Kenya wild cat, confirming they are domestic cats (Figure 2). The ancestors of indigenous cats from EAC-Lamu and Iran then diverged from ancestors of other domestic cat breeds, suggesting an early split possibly before the recent breed formation. The two sister clades formed by Iranian and EAC-Lamu indigenous cats further confirms their close relationship.

3.5. *Demographic history inference*

We selected cat genomes samples with high depth coverage for PSMS analysis, except Bengal and DovenRex1 cat with 16.6X and 9.7X respectively, other breeds were more than 22X depth (Additional file

10: Table S3). The wild cat exhibited different demographic trajectories with an early divergence (Figure 3). Iranian and EAC-Lamu domestic cats exhibited similar demographic pattern. Surprisingly, Bengal displayed a different demographic history during the early Pleistocene possibly due to its historical background. We used G-PhoCS to test the historical divergence, gene flow and the direction. Our analysis selected a demographic model (Figure 4) in which there was an ancient separation between the EAC-Central Kenya wild cat and ancestor of domestic cats coupled with mutual gene flow. This analysis further indicated that the divergent time of Iranian and EAC-Lamu domestic cats is around 2,800 years ago, followed by mutual gene flow.

4. Discussion

Our analyses provide novel insight into the influence of long distance trade on genetic diversity of domestic cats in Near East Asia and east African coast. As compared with other indigenous animals, indigenous cats from Iran and EAC-Lamu have high haplotype diversity due to their rare haplotypes (Figure 1 & Additional file 11: Table S4). All *ND5* & *ND6* sequences of Iranian and EAC-Lamu wild and domestic cats belonging to haplogroup IV (Additional file 1: Figure S1) supporting the fact that they originated from both wild and domesticated north African/southwest Asian *F. s.lybica*[2].

The relationship between Iranian and EAC-Lamu cat is further confirmed through the observed haplotype sharing pattern in the network (Figure 1 & Additional file 7: Figure S7). The high-resolution phylogeny based on genomes reveals that EAC-Central Kenya wildcat cat separated from indigenous cats from Iran and EAC-Lamu together with domestic cat breeds, further confirming they are domestic cats (Figure 2 & Figure 3). The ancestors of indigenous Iranian and EAC-Lamu cats then diverged from other domestic cat breeds suggesting an early split possibly before the recent breed formation. There are zooarchaeological evidences showing commensal relationship between cat and human before exerting influence on their breeding [31-33].

The two sister clades formed by Iranian and EAC-Lamu domestic cats further confirms their relationship till around 2,800 years ago, followed by gene flow as a result of human activities. The Indian Ocean long distance trade routes connect Southeast Asia, India, Arabia, and East Africa. Over the last 2000 years, there has been an interpenetration of cultures to East African Coast through trade consequently assimilating this coast into the international economic system [34-37]. Accessibility from the land has made the East African coast historically an integral part of Africa. This allowed movement of goods from inland to the coast and onward to international markets. Domestic cats might have been involved in this trade route between Persian Gulf and East African Coast because of their usefulness on ships infested with rodents and pest. Similarly, cat became popular and widely dispersed among Mediterranean culture as human companion pets [38].

Such kind of human assisted migration has widely been proposed for food items (chicken) and commensal stowaways (black rat). For instance, the migration of pacific rat (*R. exulans*) and the black rat (*R. rattus*) from southern East Asia to Oceania and Madagascar, respectively, more than 3,000 years ago

[39-41], supporting human activities and rats migration association. The Swahili culture indeed has its origins in the maritime oriented subsistence among African communities of this coast most of whom were Bantu speakers living in the eastern part. These early human activities might have possibly facilitated the migration and dispersal of indigenous cats between Iranian and EAC-Lamu.

Conclusion

This study provides answers to the longstanding questions concerning the influence of historical trade between Persian Gulf and East African Coast. Further, it's contributed to a better understanding of how humans have reshaped genetic diversity of wild cat, domestic cat populations in EAC-Lamu and Iran through species translocation. Our study reveals the diversity and relationship that exist between indigenous cats from Iran and EAC-Lamu. Additional cat sampling especially of wild cats and archaeological studies may provide further insights into the direction of genetic influence of this historical trade on the wild cat populations in East Africa hinterland and EAC-Lamu as well as in Persian Gulf.

Declarations

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Availability of data and materials

The datasets generated and/or analyzed during the current study are available in the XXXXXXXX.

Authors' contributions

Y.-P.Z., A.C.A., and A.E. lead the project, and designed and conceived the study. A.C.A, M.-S.P., A.E., and S.C.O. prepared the manuscript. A.C.A., W.Y, N.H.A, and L.Y.-H, performed the data analysis. A.B.R, C.H, A.C.A., W.Y, N.H.A, and L.Y.-H, performed sampling and experiments. All authors revised and approved the final manuscript.

Ethics approval and consent to participate

The animal procedures were approved by Animal Care and Use Committee of Kunming Institute of Zoology (SMKX2017007)

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

Abbreviations

EAC-Lamu: East African coastal-Lamu; ML: Maximum likelihood; PSMC: Pairwise Sequentially Markovian Coalescent; D-loop: displacement loop; G-PhoCS: Generalized Phylogenetic Coalescent Sampler.

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Figures



Figure 1

Median-joining networks for ND5 & ND6 sequences of wildcat and domestic cat from EAC-Lamu, Iran and Near East and Central Asia. Sizes of the circles are proportional to haplotype frequencies. EAC-Lamu (black), Iran (green), Near East and Central Asia (Group IV) (purple) [2]. The light blue color represents wildcat cat from EAC-Lamu.

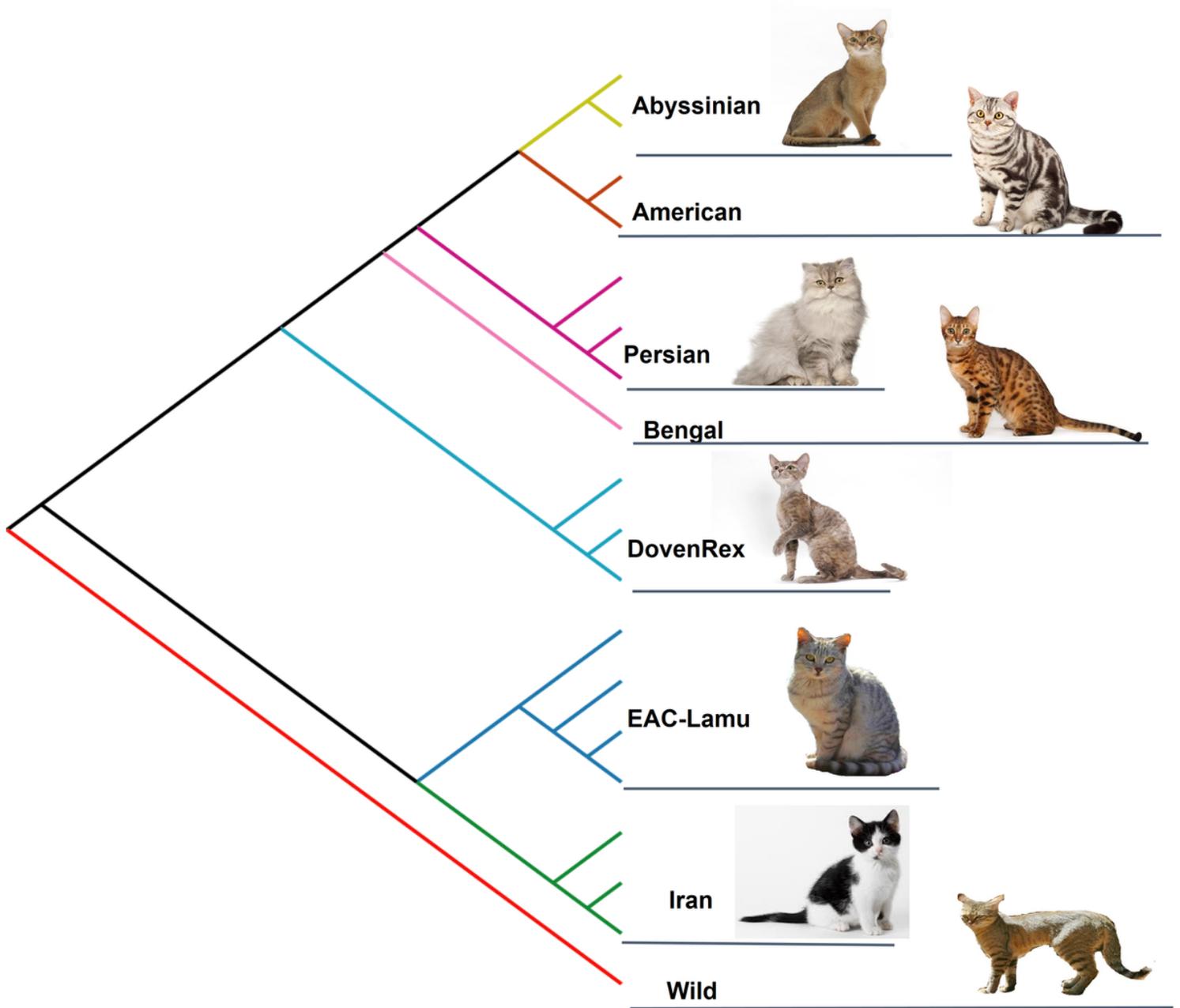


Figure 2

Maximum-Likelihood phylogenetic tree constructed using whole-genome SNPs data of wildcat and domestic cat from EAC-Lamu, Iran together with 11 domestic breed cats including three Persian cat, two American cats, two Abyssinian cats, three DovenRex cats and one Bengal cat.



Figure 3

Demographic history inferred by PSMC



Figure 4

Demographic history of wildcat and domestic cat from EAC-Lamu and Iran. Demographic history was inferred of wildcat and domestic cat from EAC-Lamu and Iran using fastsimcoal2. Divergent times are shown in the right side of the diagram.

Supplementary Files

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- [AdditionalFile12TableS5.docx](#)
- [AdditionalFile6FigureS6.tif](#)
- [AdditionalFile1FigureS1.tif](#)
- [AdditionalFile5FigureS5.tif](#)
- [AdditionalFile2FigureS2.tif](#)
- [AdditionalFile4FigureS4.tif](#)
- [AdditionalFile8TableS1.docx](#)
- [AdditionalFile11TableS4.docx](#)
- [AdditionalFile10TableS3.xlsx](#)
- [AdditionalFile9TableS2.xlsx](#)
- [Supportinginformation.docx](#)
- [Appendixsupplementarymaterialandmethods.docx](#)
- [AdditionalFile13TableS6.docx](#)
- [AdditionalFile14TableS7.xlsx](#)
- [AdditionalFile3FigureS3.tif](#)
- [AdditionalFile7FigureS7.tif](#)